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A New Species of *Zorotypus* from Central Amazonia, Brazil (Zoraptera: Zorotypidae)

JOSÉ ALBERTINO RAFAEL¹ AND MICHAEL S. ENGEL²

ABSTRACT

A new species of zorapteran (Polyneoptera: Zorotypidae: *Zorotypus*) is described and figured from alates and apterous individuals captured in Central Amazonia, Brazil. *Zorotypus amazonensis* Rafael and Engel, new species, is distinguished from related neotropical species by the setation of the male vertex, the peculiar development of the male cerci, female metafemoral ornamentation, female sternites, and presence of a true Cu vein in the hind wing base (permitting for the first time an accurate homologization of hind wing veins in Zoraptera). The Brazilian zorapteran fauna is briefly summarized and the homology and phylogenetic implications of cephalic and wing venational traits are discussed. The Embiodea + Zoraptera clade is dubbed mirorder **Mystroptera** Engel.

INTRODUCTION

With only 33 living and six fossil species, the Zoraptera are the least diverse orders of insects³ (Engel, 2003a; Grimaldi and Engel,

2005). Zorapterans are enigmatic, largely ignored insects that have mystified entomologists since their discovery nearly a century ago. While presently considered an order of Polyneoptera (Anartioptera: Plecopterida)

¹Instituto Nacional de Pesquisas da Amazônia, INPA, Caixa Postal 478, 69011-970 Manaus, Amazonas, Brazil (jarafael@inpa.gov.br).

²Division of Invertebrate Zoology, American Museum of Natural History; Division of Entomology (Paleoentomology), Natural History Museum, and Department of Ecology & Evolutionary Biology, Dyche Hall, 1345 Jayhawk Boulevard, University of Kansas, Lawrence, KS 66045-7163 (msengel@ku.edu).

³The Notoptera (consisting of Grylloblattodea and Mantophasmatodea) are the second smallest order, presently with 41 living species (vide Grimaldi and Engel, 2005; treated as separate orders therein but actually representing a single lineage [Engel and Grimaldi, 2004; Grimaldi and Engel, 2005; Arillo and Engel, in press]). The recognition of Mantophasmatodea as a separate order renders Grylloblattodea paraphyletic, as the various Mesozoic grylloblattodean fossils are basal to modern Grylloblattodea + Mantophasmatodea. It is therefore only valid to consider the Mantophasmatodea as a suborder (Arillo and Engel, in press).

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and most closely allied to the webspinners⁴ (Embiodea) (Engel and Grimaldi, 2000; Grimaldi and Engel, 2005), the order has been diversely interpreted and at times considered as related to various polyneopterous orders (e.g., Kukalová-Peck and Peck, 1993; Yoshizawa and Johnson, 2005), within or sister to Paraneoptera (e.g., Hennig, 1969), sister to Eumetabola (e.g., Beutel and Gorb, 2001), or even as sister to Holometabola (Rasnitsyn, 1998), thereby spanning all major clades of neopteran insects. Diagnoses of supraspecific taxa can be found in Engel (2003b, 2004) and Engel and Grimaldi (2000, 2002) and a preliminary phylogenetic hypothesis in Engel (2003b) (refer to table 1 for the current hierarchical classification).

Adults are dimorphic, occurring as winged and eyed individuals that are usually brown to black and are the dispersive forms of each species, while the apterous and blind morphs are slightly paler in color and are the predominant type encountered. Nymphs are similar to the adults but lack pigmentation and lack spiniform setae on the metafemora. The order is principally pantropical in distribution, and geographic records are largely limited to the type localities, with few species being documented for more than one country (a result of poor sampling rather than actual evidence of high endemism, vide infra).

The order is relatively ancient, with relatively modern species reaching back into the Early Cretaceous (Engel and Grimaldi, 2002), a situation identical for its sister, the Embiodea (Engel and Grimaldi, 2006). As such, it will likely be from early fossils that the greatest insights into resolving the placement of the highly autapomorphic zorapterans will be found. Unfortunately, pre-Cretaceous fossils of these small, relatively soft-bodied insects will be a challenge to locate given the delicate conditions necessary for their suitable preservation.

While the fossil record of Zoraptera is sparse, so too is our knowledge of the living species in which most of our information derives from three North American species: *Zorotypus hubbardi* Caudell, *Z. barberi*

TABLE 1
Hierarchical Classification of Order Zoraptera

Family Zorotypidae Silvestri
Genus † <i>Xenozorotypus</i> Engel & Grimaldi
† <i>X. burmiticus</i> Engel & Grimaldi
Genus <i>Zorotypus</i> Silvestri
Incertae sedis
† <i>Z. cretatus</i> Engel & Grimaldi
Subgenus † <i>Octozoros</i> Engel
† <i>Z. acanthothorax</i> Engel & Grimaldi
† <i>Z. nascimbenei</i> Engel & Grimaldi
Subgenus <i>Zorotypus</i> Silvestri s.str.
<i>Z. amazonensis</i> Rafael & Engel, n.sp.
<i>Z. barberi</i> Gurney
<i>Z. brasiliensis</i> Silvestri
<i>Z. buxtoni</i> Karny
<i>Z. caudelli</i> Karny
<i>Z. ceylonicus</i> Silvestri
<i>Z. congensis</i> Ryn-Tournel
<i>Z. cramptoni</i> Gurney
<i>Z. delamarei</i> Paulian
† <i>Z. goeleti</i> Engel & Grimaldi
<i>Z. guineensis</i> Silvestri
<i>Z. gurneyi</i> Choe
<i>Z. hamiltoni</i> New
<i>Z. hubbardi</i> Caudell
<i>Z. huxleyi</i> Bolivar y Pieltain & Coronado G.
<i>Z. javanicus</i> Silvestri
<i>Z. juninensis</i> Engel
<i>Z. lawrencei</i> New
<i>Z. leleupi</i> Weidner
<i>Z. longicercatus</i> Caudell
<i>Z. manni</i> Caudell
<i>Z. medoensis</i> Hwang
<i>Z. mexicanus</i> Bolivar y Pieltain
<i>Z. neotropicus</i> Silvestri
<i>Z. newi</i> (Chao & Chen)
† <i>Z. palaeus</i> Poinar
<i>Z. philippinensis</i> Gurney
<i>Z. sechellensis</i> Zompro
<i>Z. shannoni</i> Gurney
<i>Z. silvestrii</i> Karny
<i>Z. sinensis</i> Hwang
<i>Z. snyderi</i> Caudell
<i>Z. swezeyi</i> Caudell
<i>Z. vinsoni</i> Paulian
<i>Z. weidneri</i> New
<i>Z. zimmermani</i> Gurney

Gurney, and *Z. gurneyi* Choe. Indeed, the order is so little understood that many seasoned entomologists have never seen zorapterans. This fact has fueled the notion that Zoraptera are cryptic, exceedingly rare, highly endemic, and occur in low abundances. Each of these assertions, however, is not

⁴The Embiodea and Zoraptera together comprise clade “Miroder **Mystroptera** Engel, new mirorder” as defined by the characters established by Engel and Grimaldi (2000).

accurate. The apparent rarity of zorapterans stems in large part from the absence of individuals seeking them or from a lack of familiarity with the order when they are stumbled across (Engel, 2004). Once a search image is developed for zorapterans, colonies can be located in almost any suitable habitat. Indeed, in the Amazon Basin zorapterans are rather common, and the Instituto Nacional de Pesquisas da Amazônia now has more than 1300 specimens collected principally during the last three years. As suggested by Engel (2001) for tropical species and as demonstrated for *Z. hubbardi* by Hinojosa-Díaz et al. (in press), species can have relatively large ranges, and appropriate environmental and substrate conditions are readily available over these expansive distributions.

In the Neotropical region the Zoraptera previously consisted of merely 17 species. We herein describe a remarkable new species from the South American tropics, representing the 34th species for the order. The new species is particularly noteworthy for the unusual development of the male cerci, which are elongate, curved, and beset with three stiff setae along their inner margins making them appear clasperlike.

MATERIALS AND METHODS

Morphological terminology follows that of Engel (2000), with homologies for apical abdominal structures based on unpublished comparative data of M.S. Engel, while the supraspecific classification follows that of Engel and Grimaldi (2000, 2002) and Engel (2003b) (table 1). The abbreviations P, T, and S are used for palpomere, tergum, and sternum, respectively. Specimens were macerated in hot 85% lactic acid and then dissected and drawn in glycerin in an excavated slide. The entire body was mounted on slides in balsam. In slide-mounted specimens the abdomen was removed and tergites and sternites were separated laterally and mounted with their external surfaces facing upward. Some sclerites were drawn after slide mounting. Type material is deposited in the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.

SYSTEMATICS

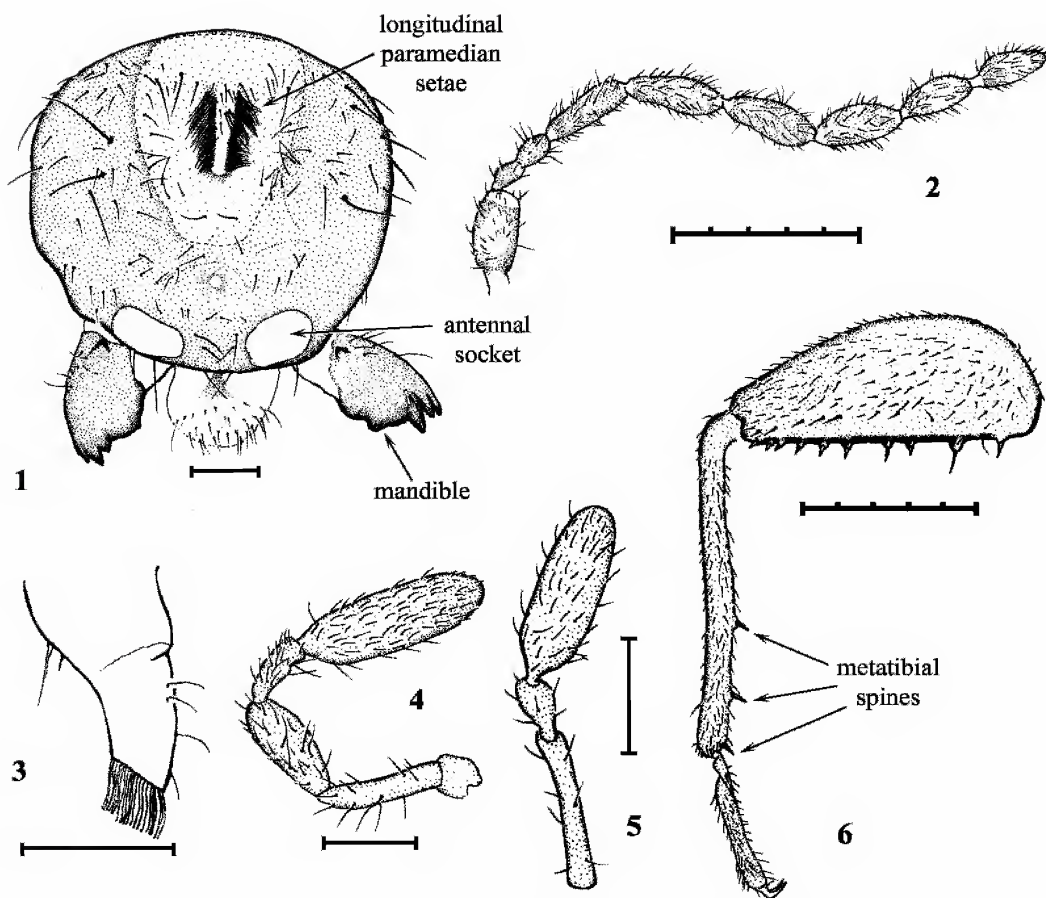
Zorotypus (Zorotypus) amazonensis, new species

Figures 1–14

DIAGNOSIS: The new species is unique for the combination of specialized, longitudinal, paramedian rows of setae on the male vertex; the clasperlike cerci of the male; the large female S8 with an apical cleft; the metafemur with 10 stiff, ventral spines and metatibia with three ventral spines in both sexes; and hind wing with a distinct and true Cu vein (vide Discussion, infra).

DESCRIPTION: Apterous male (holotype). Body length (exclusive of antennae) 2.5 mm; antennal length 1.8 mm. Integument light brown. Head subtriangular, posterior border slightly broader than pronotum; compound eyes absent, with a small black spot in position otherwise occupied by eyes; ocelli absent; head setae as depicted in figure 1; vertex with median area bordered by longitudinal, paramedian rows of pronounced, dense, slender, and divergent setae (fig. 1); antenna (fig. 2) with first antennomere cup-shaped; combined length of second and third antennomeres slightly shorter than that of first and fourth antennomeres; length of second antennomere subequal to that of third antennomere; antennomeres IV–IX longer than wide, becoming slightly shorter and paler distally. Labrum with setae in distal half (fig. 1). Mandible with three short, pointed teeth and well-defined molar region (fig. 1). Lacinia with apical comb (fig. 3). Maxillary palpus (fig. 4) five-segmented, first palpomere (P_1) short, P_2 slightly longer than P_3 , P_4 short and nearly one-half length P_3 , P_5 longest, laterally compressed, and twice as wide as P_4 , P_5 nearly as long as combined lengths of P_3 and P_4 . Labial palpus three-segmented, P_2 shortest, one-third length of P_1 and P_3 individually, P_3 laterally compressed, twice as wide as P_1 .

Pronotum subrectangular, slightly broader than long, not constricted posteriorly; longest setae on lateral and anterior margins, smaller setae scattered on disc. Mesonotum slightly smaller than pronotum, with longest setae on lateral margins. Metanotum smaller than preceding thoracic terga, distinctly wider than long, with longest setae on lateral margins.

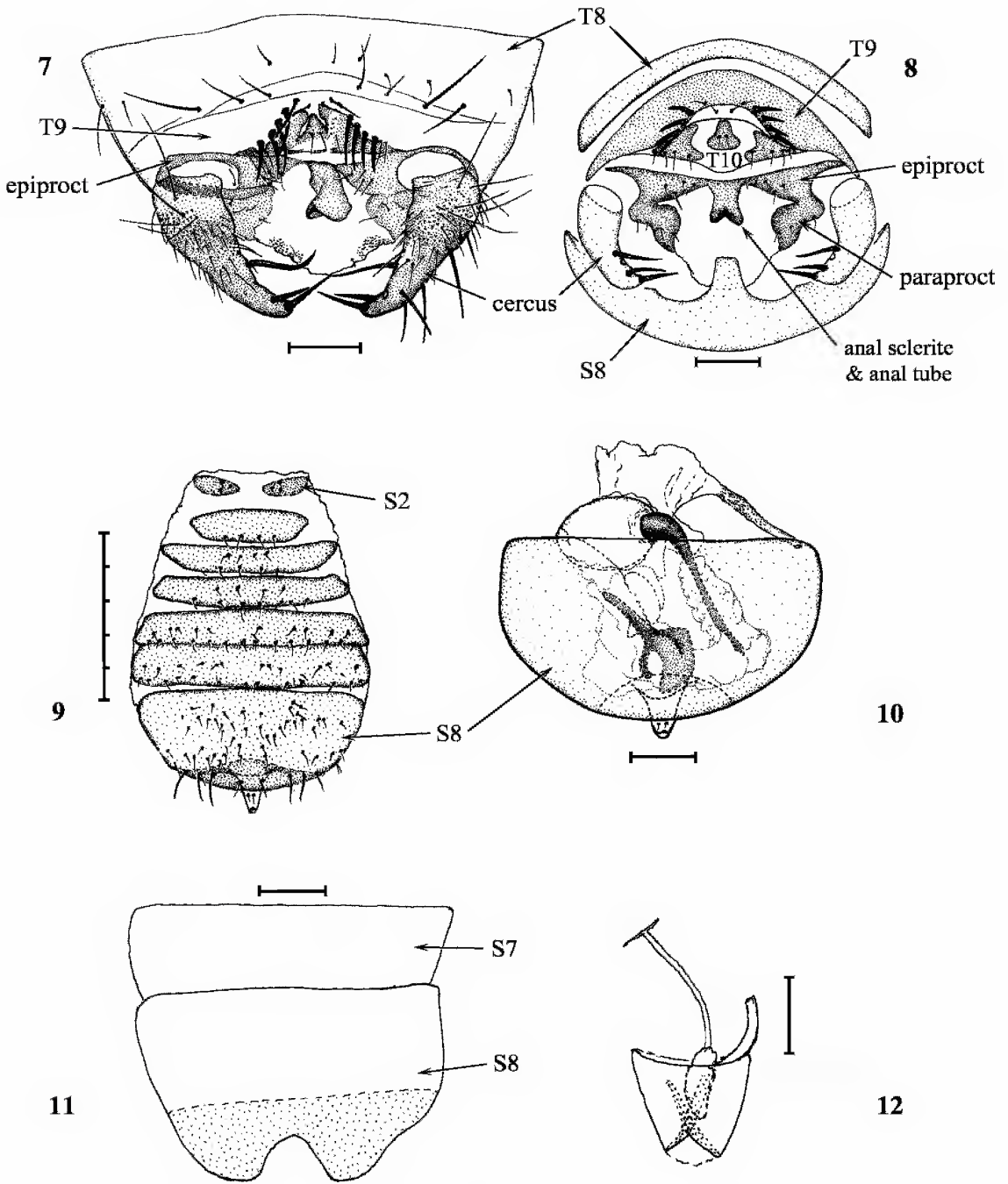


Figs. 1–6. Male of *Zorotypus amazonensis* Rafael and Engel, new species. 1. Male head, dorsal view, with antennae removed. 2. Antenna. 3. Lacinia. 4. Maxillary palpus. 5. Labial palpus. 6. Hind leg from metafemur to metapretarsus. Scale bars = 0.1 mm except that those for figures 2 and 6 = 0.5 mm.

Legs with scattered setae of moderate length, intermixed with several small setae. Pro- and mesotibiae with one and two rather stout, subapical setae ventrally, respectively. Hind leg (fig. 6) with metafemur about three times longer than broad (as measured at its point of maximal breadth), slightly more swollen toward base than apex; posterior ventral surface with 10 short, stiff spines, second spine about twice length of others, distal spines smaller and more closely spaced; metatibia with three ventral, stiff spines evenly spaced in distal half.

Abdominal T1 with single transverse row of eight setae and two small, inconspicuous lateral setae on each side of midline; T2–9 with two transverse rows of 7–10 setae each side of midline; T9 (figs. 7, 8) with small median setae dorsolaterally followed by four

thickened, rather oblique setae either side of midline and 4–5 typical setae more distally; T10 (figs. 7, 8) largely membranous, with small, median sclerite with pair of small setae, and lateral sclerites with 4–5 flanking, posterior setae; epiproct nearly divided medially, lateral portions somewhat triangular and extending around cercal base, medially strongly narrowed and fused to upcurved anal sclerite (mating hook) bearing anal tube; paraprocts broadly attached to apicolateral corners of epiproct (fig. 8). Cerci (fig. 7) unsegmented, elongate, clasperlike, with three stout, pronounced setae on inner margin, first just apical of midpoint, second subapical, third apical, all three setae directed inward; other setae rather stout, long, and along outer, lateral surface; basal half covered with short,



Figs. 7–12. *Zorotypus amazonensis* Rafael and Engel, new species, abdominal structures. 7. Male abdominal apex, dorsal view. 8. Male abdominal apex, apical view. 9. Male abdominal sterna. 10. Male sternum VIII and terminalia. 11. Female sternum VIII. 12. Female genital sclerite. Scale bars = 0.1 mm except that for figure 9 = 0.5 mm. The terms paraproct and epiproct are used here to indicate the correct sclerite homologies with other insects (based on unpublished comparative data of M.S. Engel) and in place of the less formal terms employed by Bolívar y Pieltain and Coronado (1963). The anal sclerite is fused to what we consider the epiproct in Zoraptera.

dense spicules, such spicules absent at apex and internally at base. Abdominal sterna as in figure 9; first sternum not sclerotized and apparently absent; S2 divided into small, lateral sclerites, with two pairs of small setae on each side; S3–6 with two rows of short setae, those apically and centrally slightly longer; S8 (hypandrium or subgenital plate) larger than preceding sterna (figs. 9, 10), rather oval, more sclerotized in apical portion, distal margin produced medially, protuberance with two small, subapical setae (fig. 10), setae scattered over disc and transverse row of longer setae at distal margin.

Terminalia (from paratype) as depicted in figure 10; terminalia principally membranous, highly asymmetrical, and difficult to interpret except by two pieces: central, rather club-shaped, more sclerotized portion and basal portion that is less sclerotized and bearing an apically directed, elongate, tubular projection (the tubular portion may be the same structure that forms a dorsal, somewhat sclerotized and coiled tube in four neotropical species; i.e., *Z. snyderi* Caudell, *Z. hamiltoni* New, *Z. mexicanus* Bolívar y Pielain, and *Z. cramptoni* Gurney).

Apterous female. As described for the male except as follows: body length (exclusive of antennae) 2.7 mm; antennal length 2.0 mm. Head without central, paramedian row of pronounced cluster of divergent, slender setae on vertex. Metafemur ornamentation slightly weaker than that of male. Abdominal T9–10 normal, without modifications; S8 larger than preceding sterna, slightly asymmetrical, more sclerotized in distal third, with large distal, median cleft (fig. 11). Cerci normal, small, slightly curved proximally, with rather stout setae but no spiniform setae as in male. Genital fork small, slightly sclerotized (fig. 12).

Alate female. As described for the male except as follows: body dark brown to black; compound eyes present and black; three ocelli present on vertex; venation generally reduced and weak, most veins nebulous (i.e., mostly represented by distinctly fuscous lines on otherwise hyaline or lightly infuscate membrane) although veins R, Rs, and M in forewing and R+M in hind wing at least weakly tubular for portions of their length;

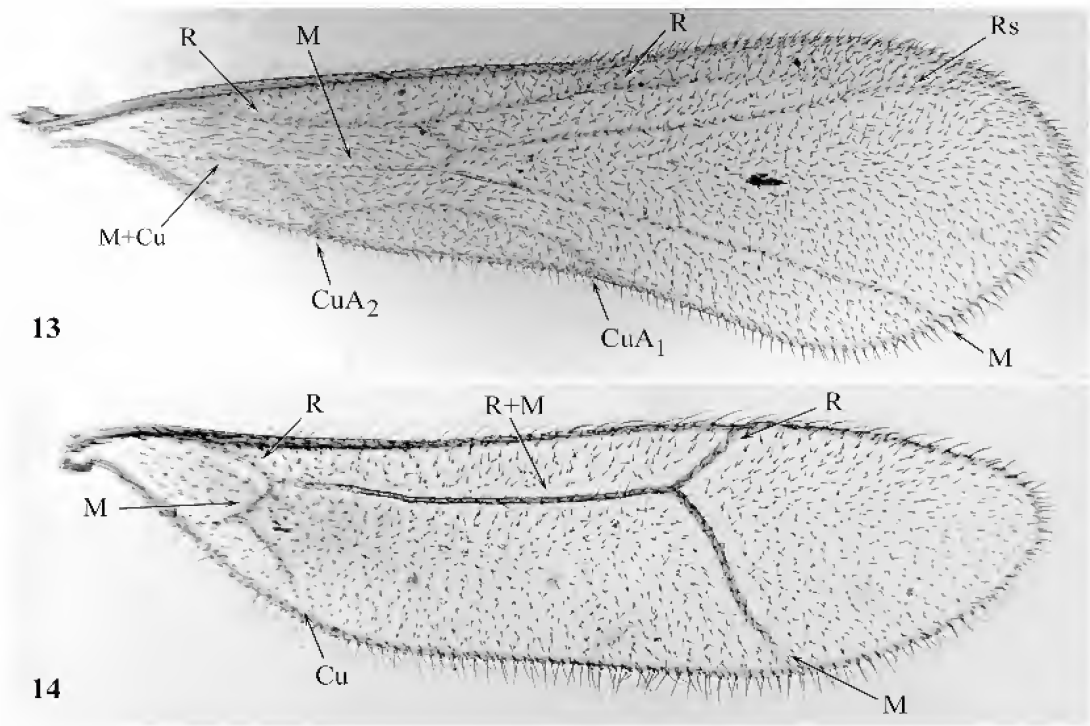
forewing length 2.7 mm, pterostigma present as faint infuscation along anterior, apical wing margin between R and Rs; R disappearing in pterostigmal base (fig. 13); Rs nearly reaching to forewing apex, becoming faint and diffuse right near apex; rs-m present (fig. 13), very short, slightly shorter than first free abscissa of Rs; M extending to posterior wing margin; CuA₁ present and extending to just beyond wing midpoint before terminating on posterior wing margin; CuA₂ present as a short stub in basal third of wing; wing setae numerous on membrane and margins, not clustered in any region of wing; additional forewing details in figure 13. Hind wing length 2.2 mm; venation typical, with stems of R and M starting separate near base and fusing for much of wing length, separating in distal third of wing, each vein terminating as evanescent vein on wing margin (fig. 14); short branch of Cu present proximally and terminating as evanescent vein on wing margin (fig. 14); exceedingly short and faint M+Cu stem present; additional hind wing details in figure 14.

HOLOTYPE: Male (slide mounted), "BRASIL, AM [Amazonas], Itacoatiara, Madeireira Mil, 17.viii.2002, J.A. Rafael & J. Vidal, sob casca de tronco caído" (INPA).

PARATYPES: One male, three females (two slide mounted, one in alcohol), same data as holotype (INPA). One alate female (slide mounted), "Manaus, Reserva Ducke, 21.ii.1992, Igarapé Barro Branco, arm. adesiva, J. Vidal" (INPA). One alate female (in alcohol), "Manaus, ZF-3, km-23, Fazenda Esteio, 18.iii.1987, B.C. Klein, armadilha malaise" (INPA).

ETYMOLOGY: The specific epithet refers to the region in which specimens were collected, i.e., Amazonia.

COMMENTS: Among Brazilian species, *Z. amazonensis* is among the most completely characterized (table 2), with both sexes and morphs documented. Within this fauna, *Z. amazonensis* is apparently most similar to *Z. shannoni* Gurney, also described from Brazil, in that both have modified and slender setae on the vertex. The organization of these setae differs prominently (vide Description, supra, and Discussion, infra), serving to separate the two species readily in the male sex. Both species also have similar metafemoral orna-



Figs. 13–14. Female alate of *Zorotypus amazonensis* Rafael and Engel, new species. **13.** Forewing (2.7 mm in length). **14.** Hind wing (2.2. mm in length).

mentation, although with 10 stiff, ventral spines in *Z. amazonensis* and six such spines in *Z. shannoni*. Likewise, both species have a membranous endophallus.

DISCUSSION

Owing to the paucity of studies on Zoraptera and the dimorphic nature of the species, comparisons across species are challenging. Species may not only be known only from a single sex, but sometimes alate forms

are unknown, hindering a comprehensive study of particular character systems. Appendix 1 summarizes the known forms of the world’s species. Despite this impediment, some preliminary conclusions can be drawn (e.g., Engel and Grimaldi, 2000; Engel, 2003b), and the discovery of *Z. amazonensis* permits some new interpretations of anatomical traits in *Zorotypus*. It is fortunate that not only males and females are known for *Z. amazonensis* but also apterous and alate forms have been recovered, permitting a more com-

TABLE 2
Checklist of Brazilian Zoraptera (updated from Rafael and Engel, in press)

Species	Sexes known	Alate known	Nymph known	Geographical records ^a
<i>Z. amazonensis</i>	♂♀	X	X	Brazil (AM)
<i>Z. brasiliensis</i>	♀	X	X	Brazil (MG, RJ, SP, PR, SC)
<i>Z. huxleyi</i>	♂♀	—	—	Peru, Brazil (AM)
<i>Z. shannoni</i>	♂	X	—	Brazil (MT, AM)
<i>Z. weidneri</i>	♂♀	—	—	Brazil (AM)

^aStates of Brazil: AM = Amazonas, MG = Minas Gerais, MT = Mato Grosso, RJ = Rio de Janeiro, SP = São Paulo, PR = Paraná, and SC = Santa Catarina.

plete characterization of this species as well as a more meaningful comparison with taxa that are similarly documented.

New (1978) noted that the cluster of setae on the vertex of *Z. shannoni* is unusual and suggested that these setae were homologous with those present on *Z. delamarei* Paulian from Madagascar. The homology of these two features, however, appears dubious given the available data (Engel, personal obs.). In *Z. shannoni* the male vertex lacks a fontanelle but has a distinct, dense, circular cluster of long, sinuous setae standing out among the usual distribution of vertical setae that are slightly shorter, straight (although not erect, frequently suberect in position), and more rigid. The vertex of male *Z. delamarei*, by contrast, has a distinct fontanelle orifice that is anteriorly bordered by a loose collection of short, sinuous setae. These setae are not congregated into a distinct patch and are generally the same size or shorter than the surrounding typical vertical setae. Indeed, the setal patch of *Z. shannoni* likely serves a glandular function during courtship in which males offer secretions from a vertical gland to the female prior to copulation (as of yet, this has not been conclusively demonstrated but appears assuredly correct based on examination of the structure), like that documented for *Z. barberi* (Choe, 1995). Such is assuredly the case in *Z. delamarei* and other species bearing a more distinct fontanelle orifice. While the gland (where observed), its secretions, and certainly the presence of a fontanelle are likely homologous, the homology of specialized setae on the vertex and surrounding and glandular openings (either as a well-defined fontanelle orifice or as small region of porous integument and clustered setae) is less obvious. It may be that numerous, species-specific modifications have arisen in order to channel or capture droplets of secretions emerging from a vertical gland as offerings to females during courtship. Alternatively, these setae may indeed prove to be homologous but may assume various forms in different species. It seems more likely, however, that different setal configurations may unite sets of species⁵ within *Zorotypus* s. str., and that while such features may be homologous among subsets of species, these types may prove to be independent in a larger

phylogenetic context. For example, both *Z. delamarei* and *Z. congensis* Ryn-Tournel have a clearly defined fontanelle and, aside from the presence of such an obvious orifice (e.g., vide Delamare-Deboutteville, 1951), they may be further united by the diffuse, sinuous setae anterior to the fontanelle. In *Z. barberi* and *Z. shannoni*, however, there is a different condition. The fontanelle is not clearly demarked as a distinct opening; instead, in each of these species it can be recognized as a tight cluster of modified setae on the vertex, sometimes set into a faint depressed region and clearly with porous integument (e.g., vide New, 1978; Choe, 1989). This overall form of glandular opening may be homologous between the two species, with the particular structure of the individual setae being distinctive to each (long, sinuous in *Z. shannoni*; shorter, stout, and erect in *Z. barberi*). Under this scenario, the presence of the gland and the glandular opening may be homologous across species, while the particular form of the opening and surrounding setae may only be homologous for subsets of such taxa. This is not to say at this time that *Z. barberi* and *Z. shannoni* are sister taxa (indeed the species are quite different) since the distribution of vertical structures across other *Zorotypus* is poorly documented and ultimately may alter some of the preliminary ideas developed here. However, among those few species in which the male vertex has been examined, the structures seen in these two neotropical species more closely approximate each other than either compare to the condition of the African species. Certainly a more extensive comparative study of fontanelle structures is required within a phylogenetic framework before definitive conclusions can be reached. Despite this current hindrance, these preliminary observations are tantalizing and indicate that numerous modifications await more definitive study and are likely associated with interesting aspects of zorapteran mating behavior.

⁵Note that the presence of a vertical gland has not yet been conclusively documented across the entire order, although it would seem that it is a feature of all *Zorotypus*. Alternatively, it may be that a monophyletic subset of *Zorotypus* has the vertical gland and that within this clade a diversity of forms of orifices and surrounding setae has arisen.

The vertex of *Z. amazonensis* also bears a cluster of modified setae and, like the other American species studied to date, it lacks the obvious fontanelle orifice of *Z. delamarei* and *Z. congensis*. However, despite the overall similarity of this species to *Z. shannoni*, the organization of these setae in *Z. amazonensis* is quite distinctive and utterly unique within the order. Rather than being clustered into a tight, circular patch as in *Z. shannoni* or *Z. barberi*, the setae are arranged into tight, longitudinal, paramedian rows on the vertex (fig. 1).

Aside from an unusual cephalic arrangement of setae, *Z. amazonensis* is further unique among those species for which alates are known by having a distinct branch of Cu proximally in the hind wing (fig. 14). The recognition of this vein permits the determination that the hind wing posterior stem termed when present as "Cu" by previous authors (e.g., Choe, 1989; Engel and Grimaldi, 2000, 2002) is, in fact, vein M. This partially supports the conclusion of Kukalová-Peck and Peck (1993) that this vein is part of the medial system, but we cannot agree that it represents MP, and their more elongate, hypothetical stem "MP+Cu" extending to the extreme wing base (e.g., their fig. 6) is not supported by observations of this or other species (Engel, personal obs.). There is also a short stub proximal to the separation of the true cubital vein, indicating that M and Cu are fused in the hind wing base. While most species have the short basal stem of M present (again, termed Cu by previous authors) (fig. 14), the presence of a short, longitudinal vein posterior to the main vein R+M is unique among species with documented venation. This vein branches very early in the wing base, thereby rendering the M + Cu stem extremely short and nearly imperceptible (fig. 14). The discovery of the alate of *Z. amazonensis* has thus permitted a more complete and accurate homologization of hind wing venation in Zoraptera.

The discovery of *Z. amazonensis* demonstrates that significant discoveries remain to be made in the order Zoraptera and that as-of-yet unrecognized variation exists among species within an otherwise homogenous order of insects. The presence of clasperlike cerci in the

male of *Z. amazonensis* is a remarkable autapomorphy for this species and one in which the study of the biology and functional morphology would be of great significance. The new species also highlights the need for extensive exploration of the tropical zones throughout the world for additional material and species of Zoraptera. While much work remains within the neotropical region, such fieldwork is even more intensely needed in Africa and Asia where only few, scattered records exist across vast regions with suitable, if not ideal, zorapteran habitat. The potential for new species and thereby new insights into this poorly understood order is great. Indeed, it is possible that with adequate sampling the diversity of the order may eventually more than double.

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APPENDIX 1
CHECKLIST OF WORLD ZORAPTERA

Species	Sexes known ^a	Alate known	Nymph known	Geographical records
† <i>X. burmiticus</i>	♂	X	—	Myanmar
† <i>Z. acanthothorax</i>	♂	X	—	Myanmar
<i>Z. amazonensis</i>	♂♀	X	X	Brazil
<i>Z. barberi</i>	♂♀	X	X	Costa Rica (Cocos), Dominican Republic, French Guiana, Panama, Trinidad, Venezuela
<i>Z. brasiliensis</i>	♀	X	X	Brazil
<i>Z. buxtoni</i>	?	—	—	Samoa
<i>Z. caudelli</i>	♂♀	X	X	Indonesia (Sumatra), Malay Peninsula
<i>Z. ceylonicus</i>	♀	—	X	Sri Lanka
<i>Z. congensis</i>	♂ ^b	—	X	Zaire
<i>Z. cramptoni</i>	♂♀	—	X	Guatemala
† <i>Z. cretatus</i>	?	—	—	Myanmar
<i>Z. delamarei</i>	♂♀	X	—	Madagascar
† <i>Z. goeleti</i>	♀	X	—	Dominican Republic
<i>Z. guineensis</i>	♂♀	—	—	Ghana, Guinea, Côte d'Ivoire
<i>Z. gurneyi</i>	♂♀	X	X	Costa Rica, Panama
<i>Z. hamiltoni</i>	♂♀	X ^c	—	Colombia
<i>Z. hubbardi</i>	♂♀	X	X	United States
<i>Z. huxleyi</i>	♂♀	—	—	Brazil, Peru
<i>Z. javanicus</i>	♀	—	X	Indonesia (Java)
<i>Z. juninensis</i>	♂♀	—	—	Peru
<i>Z. lawrencei</i>	♀	X ^c	—	Christmas Island
<i>Z. leleupi</i>	♀	—	X	Galapagos Islands
<i>Z. longicercatus</i>	?	—	X	Jamaica
<i>Z. manni</i>	♀	X ^c	—	Bolivia, Peru
<i>Z. medoensis</i>	♂♀	X	—	Tibet
<i>Z. mexicanus</i>	♂♀	X ^c	—	Mexico
† <i>Z. nascimbenei</i>	♀	X	—	Myanmar
<i>Z. neotropicus</i>	♀	—	X	Costa Rica
<i>Z. newi</i>	♀	—	—	Taiwan
† <i>Z. palaeus</i>	♀	—	—	Dominican Republic
<i>Z. philippinensis</i>	♀	X ^c	—	Philippines
<i>Z. sechellensis</i>	♂	X	—	Seychelles
<i>Z. shannoni</i>	♂	X	—	Brazil
<i>Z. silvestrii</i>	?	—	X	Indonesia (Mentawai)
<i>Z. sinensis</i>	♂	—	—	Tibet
<i>Z. snyderi</i>	♂♀	X	X	Jamaica, United States (Florida)
<i>Z. swezeyi</i>	♀	X	—	Hawaii
<i>Z. vinsoni</i>	♂♀	X	—	Mauritius
<i>Z. weidneri</i>	♂♀	—	—	Brazil
<i>Z. zimmermani</i>	♂♀	X ^c	—	Fiji

^aNote that while males are recorded for many sexes, the important features of the vertex and male terminalia have been largely overlooked, and thus the vast majority of these species require new study.

^bRyn-Tournel (1971) did not indicate the gender of her material; however, in her figures she clearly depicts a fontanelle on the vertex, indicating that her specimen was a male.

^cAlthough the holotypes of *Z. lawrencei* New, *Z. manni* Caudell, and *Z. philippinensis* Gurney and paratypes of *Z. hamiltoni* New, *Z. mexicanus* Bolivar y Pieltain, and *Z. zimmermani* Gurney are of the alate form, the individuals had become dealate prior to capture, and the wings for these species therefore remain unknown.

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